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Consequences of variation in predator attack for the evolution of the selfish herd

Lesley J. Morrell[1], Lottie Greenwood[1] & Graeme D. Ruxton[2]

[1]School of Biological, Biomedical and Environmental Sciences, University of Hull

[2]School of Biology, University of St Andrews

Correspondence:

Lesley J. Morrell

School of Biological, Biomedical and Environmental Sciences

University of Hull

Kingston-upon-Hull

HU6 7RX

Email: l.morrell@hull.ac.uk

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Abstract

There is a strong body of evidence that patterns of collective behaviour in grouping animals are governed by interactions between small numbers of individuals within the group. These findings contrast with study of the 'selfish herd', where increasingly complex individual-level movement rules have been proposed to explain the rapid increase in aggregation observed when prey groups are startled by or detect a predator. While individuals using simple rules take into account the position of only a few neighbours, those using complex rules incorporate multiple neighbours, and their relative distance, to determine their movement direction. Here, we simulate the evolution of selfish herd behaviour to assess the conditions under which simple and complex movement rules might evolve, explicitly testing predictions arising from previous work. We find that complex rules outperform simple ones under a range of predator attack strategies, but that simple rules can fix in populations particularly when they are already in the majority, suggesting strong positive frequency dependence in rule success. In addition, we explore whether a movement rule derived from studies of collective behaviour (where individuals use the position of 7 neighbours to determine movement direction) performs as successfully as more complex rules, finding again positive frequency dependence in rule success, and a particular role for predator attack strategy (from within or outside the group).

Introduction

Aggregation into groups is a widely observed natural-history trait, both taxonomically and across different biomes. An understanding of the selective pressures underlying animal grouping behaviours has been a dominant feature throughout the study of behavioural ecology (all four editions of the seminal textbook 'An Introduction to Behavioural Ecology' devote a whole chapter to the phenomenon; e.g. Davies et al. 2012). Aggregation often considered to arise as a response to predation (Krause and Ruxton 2002; Wood and Ackland 2007), as it carries with it a number of anti-predator benefits, including increased vigilance (e.g. Roberts 1996), dilution (reduced chance of being the individual attacked; Foster and Treherne 1981), encounter-dilution (reduced encounter rate; Turner and Pitcher 1986) and confusion effects (cognitive limitations reducing success; Miller 1922; Krakauer 1995), which act to reduce individual risk to each group member.

Individuals within groups also benefit from the mechanisms outlined by the selfish herd hypothesis (Hamilton 1971), where individuals reduce their own risk of predation at the expense of others in the group, effectively seeking cover within the group and placing other group members at increased risk. Work on selfish herds focuses primarily on the behavioural strategies ('movement rules') of individuals that generate aggregations, to explain the oft-observed phenomenon of facultative or increased aggregation in response perceived threat (Hamilton 1971; Foster and Treherne 1981; Krause and Tegeder 1994; Watt et al. 1997; Spieler and Linsenmair 1999; Viscido and Wethey 2002).

71 Perceived threat can also increase synchrony within groups (Bode et al. 2010).
72 The synchronous behaviour of large aggregations has been the focus of
73 significant research effort, in an attempt to understand how large-scale collective
74 behaviour can be brought about through interactions between individuals.
75 Theoretical (e.g. Huth and Wissel 1992; Huth and Wissel 1994; Couzin and
76 Krause 2003; Giardina 2008; Hildenbrandt et al. 2010; Bode et al. 2011a) and
77 empirical (e.g. Buhl et al. 2006; Ballerini et al. 2008a; Katz et al. 2011) evidence
78 suggests that patterns of collective behaviour in grouping animals are governed
79 by interactions between small numbers of individuals within the group. For
80 starling flocks, for example, each individual interacts with 6 or 7 neighbours on
81 average (Ballerini et al. 2008a); models incorporating interactions over similar
82 topological distances confirm collective behaviour as an emergent property of
83 the system (Hildenbrandt et al. 2010; Bode et al. 2011a; Bialek et al. 2012). Pair-
84 wise interactions in fish shoals effectively capture spatial patterns in groups of
85 up to 30 individuals (Katz et al. 2011), and locust swarms are coordinated by
86 only by short-range local interactions within a range of 13.5cm (Buhl et al. 2006).
87
88 This focus on generating large scale patterns from interactions with small
89 numbers of neighbours contrasts sharply with the study of selfish herd
90 behaviour, where research has focused on identifying movement rules that
91 result from complex interactions between increasingly large numbers of
92 neighbours (Morton et al. 1994; Viscido et al. 2002; Reluga and Viscido 2005).
93 Evolutionary simulations of selfish herds suggest that populations become
94 dominated by individuals that account for the position of much larger numbers
95 of neighbours (Reluga and Viscido 2005), but empirical evidence for selfish herd

96 movement rules is limited. Sticklebacks move towards a neighbour that can be
97 reached more quickly, rather than one that is geographically closer (Krause and
98 Tegeder 1994), and seals' movement is consistent with attraction towards a
99 single neighbour (using simple rules) rather than multiple neighbours (De Vos
100 and O'Riain 2012). In contrast, sheep movement patterns in response to threat
101 from a sheepdog are consistent with the idea that they are moving towards the
102 group centre (King et al. 2012).
103
104 A key difference between these two areas of work is that while collective
105 behaviour represents a stable level of aggregation, the selfish herd is a process of
106 (increasing) aggregation levels. However, theoretical research on the selfish herd
107 focuses primarily on the point at which stable aggregations have formed, but
108 recent work suggests that timing of predator attacks in relation to the point at
109 which prey first detect the predator and initiate anti-predator behaviour is
110 crucial in determining the success of movement rules, and that simpler rules,
111 accounting for fewer neighbours, might evolve under a range of biologically-
112 plausible conditions (Morrell and James 2008; Morrell et al. 2011a). While it is of
113 course feasible that the different situations of movement synchronisation and
114 increasing aggregation use different methods of processing information, the
115 discrepancy in research activity is worthy of further investigation.
116
117 In our previous work, we found that simpler mutant aggregation strategies
118 (rules) experienced a reduced share of the risk in populations of more complex
119 rules, when predators attacked during the process of aggregation (Morrell et al.
120 2011a), and in populations that are of lower density (Morrell et al. 2011b) and

121 larger size (Morrell & James 2008). More complex rules are more effective at
122 reducing risk in larger and denser populations (Morrell & James 2008, Morrell et
123 al. 2011b) and when predators attack later in the movement sequence (Morrell
124 et al. 2011a). Complex rules are also more effective at moving individuals from
125 the periphery of a group to the centre (Morrell et al. 2011b), where they will be
126 protected from predators that attack from outside the group (for a discussion of
127 predator attack strategies, see Morrell and Romey 2008; Morrell et al. 2011a and
128 2011b). We use the terms 'simple' and 'complex' rules to reflect the terminology
129 used in previous papers in this field. There has been no investigation into
130 whether these rules are cognitively 'simple' or 'complex' for animals, and this
131 may differ between species (discussed in Morrell and James 2008; Morrell et al.
132 2011a; 2011b). Essentially more complex rules appear to require individuals to
133 obtain a greater amount of information from their environment in order to apply
134 them.
135
136 Our previous work (Morrell & James 2008, Morrell et al. 2011a, b) provides a
137 series of predictions, based on reduction of individual risk in a group, as to when
138 mutant individuals using simpler rules should be able to invade a population of
139 more complex rules. Here, we explicitly test those predictions in an evolutionary
140 simulation model, to explore whether the reduction in risk translates into
141 fixation in a population over evolutionary time. Our first aim, therefore, is to test
142 the following predictions arising from previous work:
143 1. Predators that attack from the periphery favour the evolution of complex
144 movement rules in prey

2. When predators attack early in the movement sequence (i.e. shortly after they are detected, and when individuals have had little time to move in response to detecting the predator), simple strategies are favoured, while predators that attack later favour the evolution of more complex strategies.
3. Variation in attack timing (i.e. when predators can attack both quickly and more slowly after prey initiate aggregation) should favour the maintenance of mixtures of strategies within the population (following from prediction 2).
4. Simple rules are favoured in large, low-density populations, while complex rules are favoured in small, compact populations.

Our second aim (which could be considered a special case of the more general aim 1) is derived from the substantial body of work on collective behaviour (e.g. Couzin and Krause 2003; Ballerini et al. 2008a; Giardina 2008; Hildenbrandt et al. 2010; Buhl et al. 2011; Katz et al. 2011; Bode et al. 2011a; Bialek et al. 2012), and is to specifically assess whether a rule whereby individuals move towards 7 neighbours might perform as effectively as more complex rules in reducing individual risk. This leads to the prediction that:

5. A rule whereby individuals account for the position of 7 neighbours (i.e. a relatively small number) is as likely to evolve as a more complex rule whereby individuals account for the position of up to 20 individuals (the "Local Crowded Horizon" rule; Viscido et al. 2002, table 1).

Materials and Methods

We used an agent-based modelling framework used in previous work on selfish herd behaviour (James et al. 2004; Morrell and James 2008; Morrell et al. 2011b; Morrell et al. 2011a) as the basis for our evolutionary simulation. In each generation of the model, N point-like agents representing the prey individuals are randomly placed (following a uniform random distribution) into a circular arena of radius R m, giving a prey density $d = N/\pi R^2$. We assume that the habitat is homogeneous and provides no areas of cover that could be used to reduce predation risk: in accordance with (Hamilton 1971), cover is provided by position relative to other individuals only, and prey receive no directional information regarding predatory threat (Hamilton 1971; Morton et al. 1994; Viscido et al. 2002; James et al. 2004; Morrell and James 2008; Morrell et al. 2011b; Morrell et al. 2011a). We consider $N = 20$ and $d = 4$ as our 'baseline' parameter values, and explore the independent effects of increasing group size ($N = 50$) and increasing density ($d = 10$).

Each prey is allocated a movement rule, selected from those previous proposed. We consider 4 movement rules here, following previous work on the topic. Firstly, we consider the 3 rules investigated by Morrell et al. (2011a) and Morrell et al. (2011b): nearest neighbour (*NN*), 3 nearest neighbours (*3NN*) and local crowded horizon (*LCH*). These rules are described in table 1. To investigate whether rules that account for 7 neighbours are competitive against those that account for more (prediction 4), we also include a 7 nearest neighbour rule (*7NN*) in our investigations. Although previous work has considered 'random movement' as a potential rule, we do not include it here as it is well established that all other rules are beneficial in relation to random movement (Morton et al.

194 1994; Viscido et al. 2002; Morrell and James 2008). In each generation, N_p
195 individuals are allocated a 'population' movement rule, and N_m are allocated a
196 'mutant' movement rule ($N_m + N_p = N$). We explore 2 different starting
197 combinations: a single mutant in a population using a different rule ($N_m = 1$, $N_p =$
198 N-1), and a situation where both rules begin at equal frequencies ($N_m = N_p =$
199 $N/2$). These two scenarios represent two possible events: a mutant rule arising
200 by chance in an existing group, and a situation where two groups, using different
201 rules, meet. Throughout, we refer to the 'simpler rule' as the one that requires
202 information about the position fewer neighbours, and the 'more complex rule' as
203 one that require information about more neighbours (table 1).
204
205 As in previous work, the start of the simulation (timestep $t = 0$) represents the
206 point in time at which the prey first detect the predator and movement begins.
207 We assume that all individuals detect the predator simultaneously and begin
208 moving, following Hamilton (1971), Morton et al (1994), Viscido et al. (2002)
209 and Morrell and James (2008). The end of the simulation occurs at time T, which
210 is the point at which the predator attacks the prey. In each timestep t (t=0.1 s),
211 each prey individual identifies its target location, dependent on its allocated
212 movement rule and moves at a speed of 0.15 m s^{-1} towards the target location
213 (representing the movement speed of a three-spined stickleback, following
214 James et al. 2004). All individuals move simultaneously, and update their target
215 location in each timestep. At time T ($T > 0$) the predator appears, and attacks the
216 closest prey item. T takes either fixed values (T = 20, 50 and 100 are used here)
217 or is randomly drawn from a uniform distribution between 0 and T_{max} (T_{max} = 50,
218 100).

We investigate two predation strategies *P*: the predator may appear within the group (following Hamilton 1971) or may appear outside the group (empirical evidence for these strategies is reviewed in Morrell and Romey (2008) and discussed in Morrell and James (2008) and Morrell et al. (2011a, 2011b) in the context of the selfish herd). If the predator appears within the group, we calculate the mean group centre from the x and y coordinates of the prey at *T*, and the maximum distance of all prey from the mean group centre. The predator is placed at random within the circle described by these two parameters, following a uniform distribution. Predators attacking from outside the group appear at the edge of the circular arena (distance *R* from the arena centre), at a location determined by an angle drawn from a random uniform distribution.

Once the predator location has been determined, the predator attacks the closest prey item. We assume that an attack always occurs, and that all attacks result in successful predation. The movement rule of the predated individual is recorded. For simplicity, we assume that only one individual is predated, and that individual is replaced in the next generation. To determine the movement rule of the replacement individual, we calculate the proportion of surviving individuals using each rule. If a random number drawn from a uniform distribution between 0 and 1 is less than N_m/N, the replacement individual follows the mutant movement rule; otherwise it follows the population movement rule. N_m and N_p are updated in each generation for a total of 5000 generations, or until the population fixes at a single movement rule (N_m or $N_p = N$). This final movement rule is recorded, or, if a mixture of movement rules still remains (N_m and $N_p > 0$),

this fact is recorded. For each combination of movement rules, and for each set of parameter values (see below), we ran 1000 replicates to give a final output of the number of replicates ending in each of the three possible outcomes: mutant rule fixes, population rule fixes, and mixture of rules remains. We standardised the starting positions of both prey and predators for each combination of movement rules and set of parameter values (Morrell et al. 2008), such that each set of 1000 replicates x 5000 generations was run with the same set of initial positions for both predators and prey.

We compare the frequency at which each rule becomes fixed against random expectation i.e. the proportion of simulations in which a rule is expected to fix if predation is independent of movement rule (i.e. through drift). The probability of such a 'neutral' mutant rule becoming fixed is equal to its frequency in the population at the start of the simulation (i.e. N_m/N, Kimura 1962). Statistical comparisons between model output and the expected frequency were made using binomial tests (R v2.12.2, R Development Core Team 2011), corrected for multiple testing (180 tests were run) using a Bonferroni correction. These results are displayed on the figures. We found essentially similar results to those represented here when we re-ran the model with different combinations of parameter values caused by different discretization of strategy-space, so can be relatively confident our results are robust in this regard. Our key findings are summarised in table 2.

In contrast to previous work (Hamilton 1971; Morton et al. 1994; Viscido et al. 2002; James et al. 2004; Morrell and James 2008; Morrell et al. 2011b; Morrell et

al. 2011a) we do not explicitly calculate the Domain of Danger (DOD; Hamilton 1971) or limited DOD (LDOD; James et al. 2004) for each individual. This is implicitly captured in our assumption that predators target the nearest individual, as the DOD describes the space around each individual that is closer to it than to any other individual. Thus, when a predator attacks the closest individual, it is by definition within the DOD of that individual.

Results

(a) Invasion success and predator attack strategy

Firstly, we investigated the effect of predator attack strategy (from within the group or from outside it, prediction 1) and fixed attack time T of 20, 50 and 100 timesteps (equivalent to 2, 5 and 10 s, prediction 2) on the proportion of simulations ending with the fixation of each rule. We find that in general, complex populations (groups where the field strategy is complex) are highly stable against invasion by a single simpler mutant (figure 1a, d and g), with only occasional instances of 3NN mutants becoming fixed in LCH populations (figure 1g). Otherwise, successful invasions by simpler rules are consistent with random expectation, or worse. When both rules begin at equal frequencies (figure 1b, e and h), the complex rule is likely to outcompete the simpler one and reach fixation more often than expected by chance. The exception to this is at short attack times when predators attack from within the group, when NN strategies can reach fixation against LCH (figure 1e) at a rate consistent with chance, and 3NN reaches fixation at the expense of LCH (figure 1h). Logically, this is sensible: in a short period of time, an individual moving towards a dense but more distant area of a group makes little immediate progress towards a near neighbour

294 (remaining isolated for longer), while an individual moving directly to that
295 neighbour reduces its risk rapidly (Morrell and James 2008).
296
297 More complex mutants can successfully reach fixation more often than expected
298 by chance in simpler populations (groups where the field strategy is simple)
299 (figure 1c, f and i), but they do not dominate the results, suggesting that simple
300 populations can be stable against single, more complex mutants. This is
301 particularly true when predators attack from the inside, when attack times are
302 shorter, and when the difference in rule complexity is smaller (i.e. NN v 3NN and
303 3NN v LCH, but less for NN v LCH). At fixed attack times, as expected, we see very
304 few situations where a mixture of rules is maintained in the population: the only
305 instance of this occurring is seen in figure 3h, at $T = 100$ and when predators
306 attack from within the group (see table 2 for a summary).
307
308 ***(b) Fixed versus variable attack timing***
309 Next, we investigate the effect of variable attack timing (where attack timing is
310 drawn from a uniform distribution between 0 and T_{max}) on the fixation of rules
311 (prediction 3). As we previously (figure 1) showed that mixtures might be
312 favoured particularly when groups start with equal frequencies of the two rules,
313 we explore this starting combination here. We find no evidence to suggest that
314 mixtures of rules are maintained in the population when attack time T is variable
315 (i.e. drawn from a random uniform distribution) for any pairwise combination of
316 movement rules at any of the three group size and density parameters we tested
317 (figure 2).
318

(c) Effects of population size and density

We did, however find that population size and density influenced the success of different rules (prediction 4, figure 2). Increasing the size of the population (comparing the left hand column of figure 2 where $N = 20$ to the central column where $N = 50$) favours simpler rules at short attack times, for NN v LCH (at the shortest attack time $T = 20$) and 3NN v LCH (at attack times $T = 20$, $T = 50$ and both variable timings, but not at $T = 100$, where LCH is favoured by increasing population size). Simple rules are not favoured by increasing population size for NN v 3NN where 3NN is increasing favoured as group size increases (figure 2b), or for NN v LCH, where LCH remains superior at attack times other than $T = 20$. Increasing the density of the population (right hand column of figure 2) slightly favours the fixation of more complex rules across all rule combinations.

(d) Effectiveness of 7NN

Both 7NN and LCH populations are generally stable against mutants using the alternative rule (prediction 5, figure 3). In LCH populations, 7NN may come to dominate in a small proportion of replicates, especially when predators attack from within the group (figure 3a-c). 7NN populations, on the other hand, are stable except when predators attack from outside the group, when LCH can invade a small proportion of the time (figure 3g-i). Increasing density reduces slightly population stability for both rules (figure 3c and i), but increasing population size benefits only LCH mutants. When the rules begin at equal ratios (figure 3d-f), 7NN fixes in a larger proportion of replicates when predators attack from within the group, while LCH fixes in the majority of simulations when predators attack from outside the group. This is particularly true at increased

344 population sizes (figure 3e) and differences are less marked in denser groups
345 (figure 3f).
346
347 **Discussion**
348 A key motivation for our study was a growing apparent incongruity in the
349 literature. On one hand, much of the theoretical literature on behaviours
350 underlying the selfish herd, including our results here, suggests that cognitively
351 more complex behavioural rules generally outperform simpler rules (Viscido et
352 al. 2002; Reluga and Viscido 2005; Morrell and James 2008; Morrell et al. 2011a).
353 On the other hand, empirically based works suggest that in most taxa studied the
354 behaviours that appear to underlie the formation and especially maintenance of
355 groups appear to be relatively simple, involving responsiveness to only a small
356 number of neighbouring individuals (Couzin and Krause 2003; Ballerini et al.
357 2008b; Ballerini et al. 2008a; Hildenbrandt et al. 2010; Katz et al. 2011; Bode et
358 al. 2011a; Bialek et al. 2012). Here we have been able to offer pointers towards a
359 resolution of this incongruity. In particular we show that the performance of
360 individuals with particular behaviours within a group is strongly positively
361 frequency dependent. Thus under a wide range of the situations explored in this
362 study we find that a mutant with a more complex movement rule can fail to
363 invade a population with a simpler rule, even in circumstances where the
364 complex rule would be evolutionarily stable to reinvasion by the simpler one if it
365 did reach numerical dominance in the population. Hence, if it is the case the
366 simple aggregation-linked movement rules are a common evolutionary
367 intermediate stage in the development of more complex rules, then this strong

368 positive frequency dependence may mean that initial flourishing of simple rules
369 stops subsequent evolutionary spread of complex rules.
370
371 Although the idea that complex aggregation rules evolve from simpler ones is
372 highly plausible (Reluga and Viscido 2005), our results point to the considerable
373 benefit this field would gain from increasing our understanding of the evolution
374 the cognitive underpinning of such rules to test this conjecture. Little is known
375 about the relative costs of the different rules in relation to their apparent
376 complexity. Complex rules may carry cognitive costs associated with, for
377 example, information gathering either before or during a predation event, and
378 we suggest there is an urgent need for empirical investigation of the costs and
379 benefits of different movement rules, and for an evaluation of the effects of these
380 costs on the potential for different rules to evolve in nature.
381
382 Despite the pattern of strong positive frequency dependence in rule success, we
383 do find evidence that changing conditions (predator attack strategy, attack
384 timing and population size and density) shift the balance of rule success (Morrell
385 et al. 2011b; Morrell et al. 2011a). In line with our predictions we find some
386 evidence that peripheral attack strategies are more likely to favour the evolution
387 of complex rules (prediction 1, figure 1), and that those complex rules are more
388 likely to be favoured at later attack times (prediction 2, figure 1). We find no
389 evidence, however, that variation in attack timing supports the coexistence of
390 rules within a population (prediction 3, figure 2). We find that increased
391 population size and lower population density may sometimes improve the

392 success of simple rules, although this is not always the case (prediction 4, figure
393 2).
394
395 With respect to our prediction that 7NN and LCH are similarly successful, we find
396 partial support. The positive frequency dependence pattern is particularly strong
397 here, with successful invasions of single mutants occurring at low frequencies
398 under the majority of parameters assessed here. However, we see a particular
399 effect of predator attack strategy here in the equal ratios scenario: LCH
400 outperforms 7NN when predators attack from outside the group, while 7NN
401 succeeds when predators attack from within the group. This likely arises because
402 the more complex a rule is, the more effective it is in allowing individuals to
403 reach the centre of the group (Morrell et al. 2011b), where they are protected
404 from peripheral predators, while simpler rules allow for rapid reduction in
405 individual risk when predators attack from within the group (Morrell & James
406 2008, Morrell et al. 2011a). Thus, 7NN (as the simpler of the two) is favoured
407 when predators attack from within the group, and LCH (as the more complex)
408 when predators attack from outside.
409
410 Notice that our consideration of the relative fitness of different strategies
411 considers only within-group differences in expected fitness – and not between-
412 group heterogeneity in predation risk. This is because a key assumption of the
413 selfish herd hypothesis is that there is no group-level variation in predation risk
414 (Hamilton 1971). Our simulations assumed that predators always attack and
415 attacks are always successful, thus any benefits that one individual in a group
416 gains from cover seeking through the selfish herd comes at the expense of

417 increasing predation risk felt by one or more group-mates. This greatly simplifies
418 the scenarios that need to be explored in evaluating the likely evolutionary
419 trajectory of different behavioural rules. Specifically the per-capita average
420 predation risk of individuals in a group is independent of the distribution of
421 strategies played by individuals within that group, and so in considering whether
422 one strategy will prevail evolutionary, we need only consider the comparison of
423 strategies within a group without the added complicity of differential
424 performance of groups with different strategy mixes. Most importantly, if a
425 complex rule rose to numerical dominance within one group, we would not
426 expect this to allow that group to flourish differentially with respect to groups
427 using a simpler rule.
428
429 Our work also points to other ways in which the behaviours underlying group
430 formation through selfish herd effects might usefully be explored. In common
431 with all previous works we consider situationally-unresponsive rules (Hamilton
432 1971; Morton et al. 1994; Viscido et al. 2002; James et al. 2004; Reluga and
433 Viscido 2005; Morrell and James 2008; Morrell et al. 2011b; Morrell et al. 2011a).
434 That is, a given individual employs the same rule regardless of the situation it
435 finds itself in. However, it is easy to imagine that individuals could modify the
436 rule they use to drive their behaviour according to any number of factors:
437 including the size of the group they are in, population density, their position
438 relative to the group centre, time since the predator was first detected,
439 information transfer through the group (Bode et al. 2011b) and behaviours
440 observed in other individuals. As a simple example, an individual might utilise
441 one rule if it perceives that it is one of the first individuals to detect a predator,

442 and another rule if it perceives that it is one of the later-responders. It would be
443 interesting to explore whether a suite of simple situationally-responsive rules
444 can outperform a single more complex but situationally-unresponsive rule.
445
446 Another interesting issue worthy of further exploration is the ecological
447 robustness of rules. Different taxa will experience differences in the intensity and
448 nature of variation in predation scenarios encountered, but strict uniformity of
449 encounter of the type considered in most of our and previous theoretical
450 situations will not be the norm. That is, in the context of the scenario explored
451 here, a given individual may (over its lifetime) experience variation in the
452 number of individuals with which it might potentially form an aggregation, the
453 initial spatial density of those individuals, the time interval between first
454 detection of the predator and completed attack, and the position of the predator
455 relative to prey individuals at the point of first detection. One possible way to
456 cope with such environmental variability would be to have situationally-
457 responsive rules of the type discussed above, and (for example) behave
458 differently when in a low-conspecific-density situation to a high-density one.
459 However, it may be that sometimes conspecific density (in this case) is difficult
460 for individuals to evaluate, and individuals do best of have a "robust" behavioural
461 rule which performs well when evaluated across the frequency distribution of
462 different environmental circumstances likely to be encountered by individuals.
463 Hence, another exciting avenue for the exploration of behavioural rules
464 underlying selfish herd aggregation behaviours is how environmental variation
465 in the types of predator-prey encounters experienced selects for either
466 situationally-responsive strategies of the type discussed above, or robust

strategies that would not be evolutionarily stable in a uniform environment of one fixed type of predator-prey encounter but which offer good performance when evaluated over a frequency distribution of different encounter types.

One last avenue worthy of exploration is error-tolerance. In common with previous works, our evolutionary simulations assume that individuals utilising a particular rule can gather all the information on conspecifics needed for the implementation of that rule without error. This is likely to be a simplification of reality, and it would be interesting to explore how the introduction of different plausible error structures influences the relative performance of different rule types. For example, it may be that errors in the evaluation of another individual increase with increasing distance of that individual from the focal individual. If errors are common and essentially independent when evaluating information on different individuals this may select for more complex rules that obtain stochastic cancellation of such errors (the "many wrongs principle" – discussed in the literature on in group navigation decisions e.g. Simons 2004; Hancock et al. 2006; Biro et al. 2006; Codling et al. 2007; Faria et al. 2009). Additionally, errors may be influenced by environmental factors such as ambient light levels. This may offer the opportunity for empirical testing of theoretical predictions about how behavioural rules might be expected to change in response to increased error rates in information gathering (say as induced experimentally by lowering ambient light levels).

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604

605 **Figure legends:**

606 **Figure 1**: Number of simulations resulting in fixation for the simpler (white
607 shading), more complex (grey shading), or neither (black shading) rule, for 3
608 scenarios (columns) and three movement rule combinations (rows). Each
609 column represents a different invasion scenario: a simple rule invading a more
610 complex population (left hand column, a, d and g), a more complex rule invading
611 a simple population (right hand column, c, f and i), and a situation where both
612 rules begin at equal frequencies (central column, b, e and h). Each row
613 represents a different pairwise combination of movement rules: NN v 3NN (top
614 row, a-c), NN v LCH (middle row, d-f) and 3NN v LCH (bottom row, g-i). In each
615 case the simpler rule is specified first (see table 1). The horizontal dashed line
616 represents the expected proportion of simulations in which the simpler rule
617 would be expected to fix if predation were random with respect to movement
618 rule, ** indicates significant deviation from random expectation at $p < 0.001$, NS
619 indicates no significant deviation from random expectation. Each panel shows
620 the outcome for 3 different fixed attack times (20, 50 and 100 timesteps) when
621 the predator attacks from within the group (left of the thick vertical line) and
622 from outside the group (right of the thick vertical line). Other parameters: N =
623 20, d = 4.

624

625 **Figure 2**: Number of simulations resulting in fixation for the simpler (white
626 shading), more complex (grey shading), or neither (black shading) rule, for three
627 movement rule combinations and when predators attack from within the group.
628 Each panel shows both fixed (left of the thick vertical line) and variable (right of

629 the thick vertical line) attack timings for populations of N = 20 (left column, a, c,
630 e) and N = 50 (right column (b, d, f). Three combinations of rules are shown, both
631 begin at equal frequencies in the population: top row: NN v 3NN, middle row: NN
632 v LCH, bottom row: 3NN v LCH. Results are shown at three different population
633 size/density combinations: left column: N=20, d=4 (baseline), middle column:
634 N=50, d=4 (increased population size) and right column: N=20, d=10 (increased
635 population density). The horizontal dashed line represents the expected
636 proportion of simulations in which the simpler rule would be expected to fix if
637 predation were random with respect to movement rule, ** indicates significant
638 deviation from random expectation at $p < 0.001$, NS indicates no significant
639 deviation from random expectation.

640

641 **Figure 3**: Number of simulations resulting in fixation for the 7NN (white
642 shading), LCH (grey shading), or neither rule (black shading) for pairwise
643 contests between 7NN and LCH, for 3 invasion scenarios (rows) and three
644 population size and density combinations (columns). The left column shows data
645 for N=20, d=4 (a, d, g). In the middle column group size is increased to N=50
646 while keeping d=4, and in the right column density is increased to d=10 while
647 keeping N=20. The top row shows a 7NN mutant against and LCH population,
648 while the middle row shows the results from equal starting frequencies, and the
649 bottom row shows an LCH mutant in a 7NN population. Each panel shows both
650 fixed and variable attack times (x-axis) and predators that attack from inside
651 (left hand columns) and outside (right hand columns) the group (separated by
652 the thick vertical line). The horizontal dashed line represents the expected

653 proportion of simulations in which the simpler rule would be expected to fix if
654 predation were random with respect to movement rule, * indicates significant
655 deviation from random expectation at $p < 0.05$, ** at $p < 0.001$ and NS indicates
656 no significant deviation from random expectation.

657

658

659 **Tables and Figures**

660 **Table 1**: Movement rules

Rule	Description
NN	Each prey individual moves directly towards its closest neighbour (Hamilton 1971). This is the simplest rule we consider, and is used in testing predictions 1-4.
3NN	Each individual moves towards the average location of its three closest neighbours (Morton *et al.* 1994).
7NN	Each individual moves towards the average location of its seven closest neighbours (Morton *et al.* 1994). This rule is used to test prediction 5 only.
LCH	Each individual takes into account the location of up to 20 closest neighbours, although closer individuals have a stronger influence on movement direction, described by the perception function $f(x) = \frac{1}{1+kx}$ where k=0.375 and x is the distance from the focal individual to each neighbour. Individuals thus move towards the densest areas of the group (Viscido *et al.* 2002). This is the most complex rule we consider.

661

662

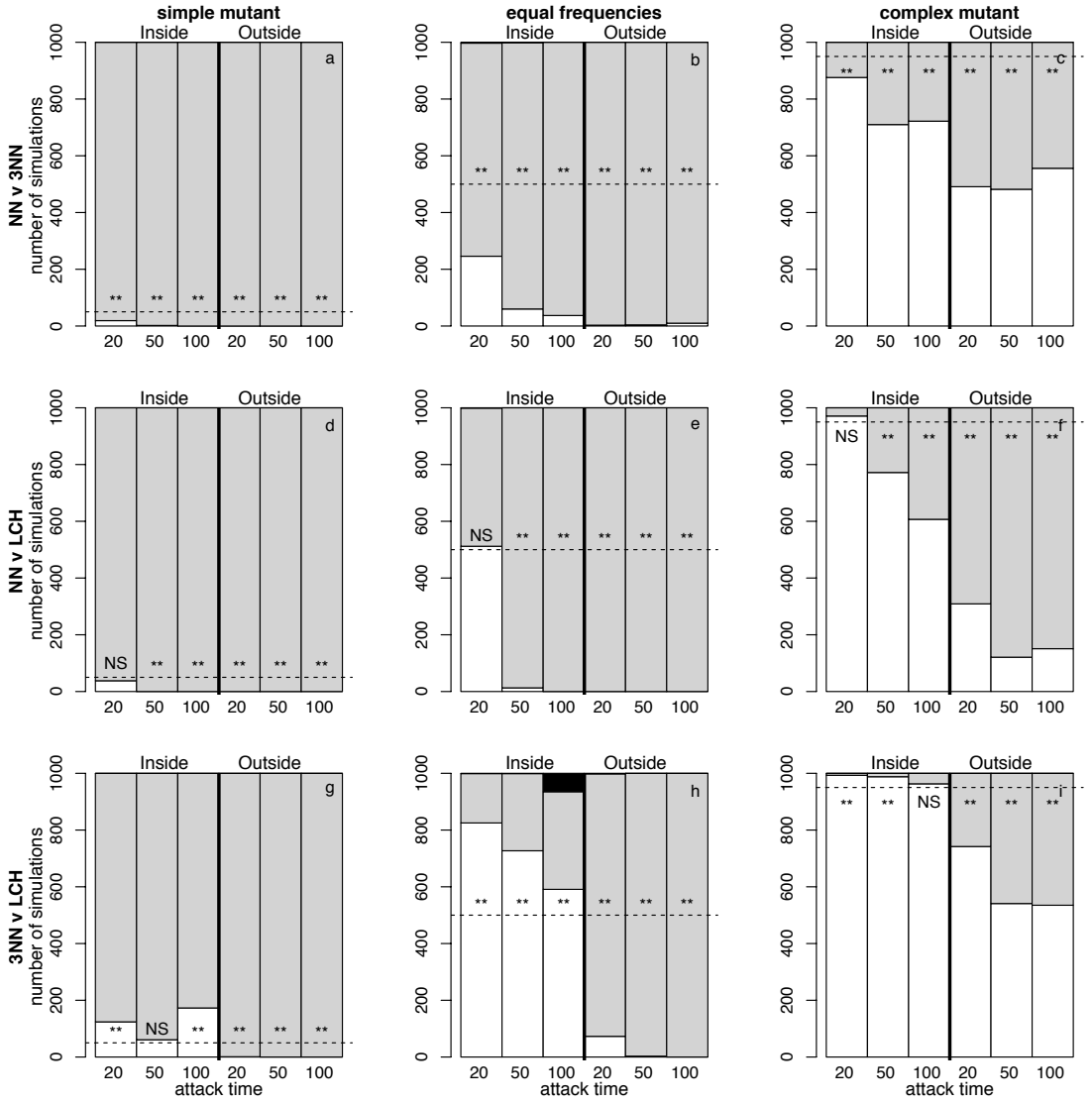
663 **Table 2:** Summary of predictions and results

664 (Please see the additional document for this table, which is formatted as

665 landscape)

666

667 Figure 1



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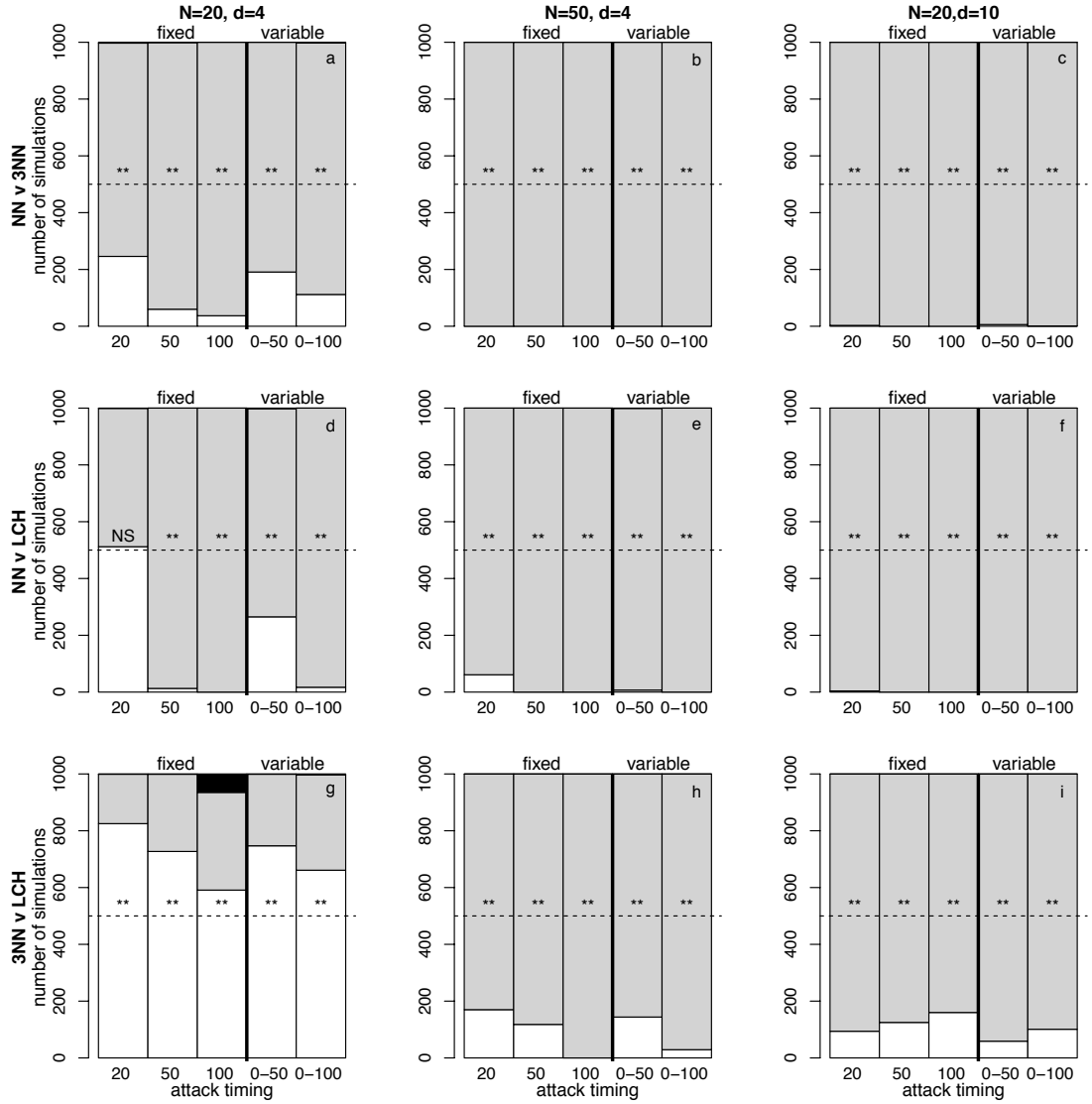
671 Figure 2



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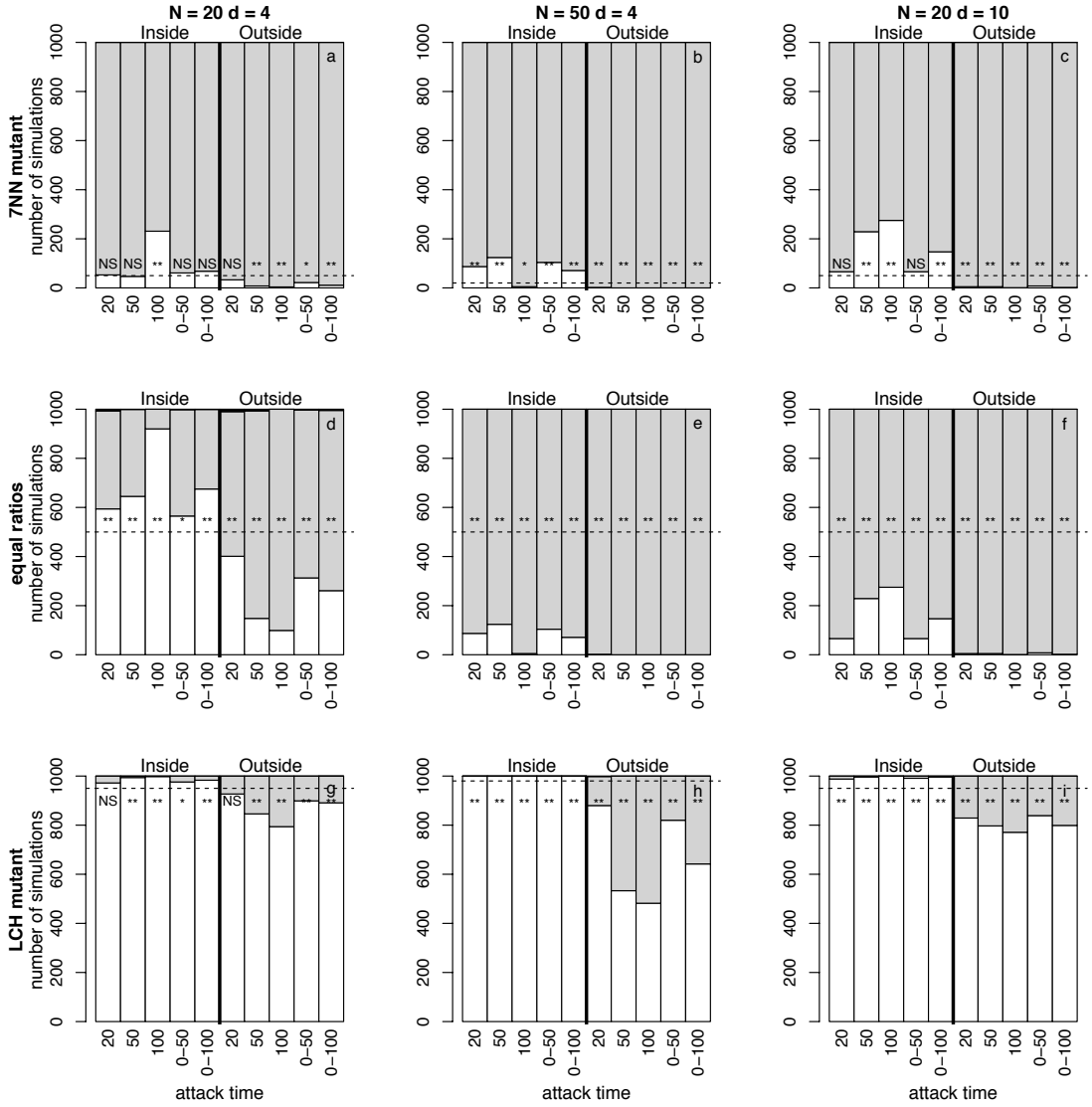
674 Figure 3



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